

MATERNAL EFFECTS AND EGG HATCHABILITY IN *MELANOPLUS* (ORTHOPTERA: ACRIDIDAE)

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Abstract.—Continuous culturing of nondiapause strains of *Melanoplus* is possible because eggs are able to hatch within a short period of time and without the requirement of cold exposure. Analysis of intercross data involving field and nondiapause strains reveals that the proportion of eggs with this property is under maternal influence and, in some cases, a function of the egg's genotype. The problem of loss of genetic variation that is often associated with laboratory strain maintenance is discussed and a solution that capitalizes on maternal effects is offered.

Key Words.—Insecta, Orthoptera, Acrididae, *Melanoplus*, hatchability, maternal effects

The central and desirable feature of the much used nondiapause strain of *Melanoplus sanguinipes* Fabr., developed by Pickford & Randell (1969), and of the recently established nondiapause strain of *M. differentialis* (Thomas) (Oma et al. 1990), is the ability of eggs to hatch in a relatively short period of time (about 21 days at 30° C for *M. sanguinipes*) without the requirement of cold treatment. In this paper the term "egg hatchability" is restricted to this usage, which in reality is equivalent to the proportion of nondiapausing eggs; indeed, it is this trait that was selected for by the developers of these nondiapause cultures. There is no doubt that egg hatchability has a heritable basis, and although the mode of inheritance is presently unknown, polygenic inheritance is likely involved judging from the slow responses to selection for the trait (Slifer & King 1961). Environmental factors, such as temperature and photoperiod (Oma et al. 1990), can also influence hatchability; these agents probably interact with genotype to account for latitudinal variations in voltinism that are observed in the United States. Maternal effects, genic or nongenetic (mediated, for example, through maternal nutrition), result in offspring with phenotypes more similar to those of the female parent than to those of the male parent (Mather & Jinks 1982). Such effects were recently suspected during hybridization experiments (WC, unpublished data) when the species status of distant populations of *M. sanguinipes* and the nondiapause strain noted were examined. To support the claim for maternal effects, an analysis of these data and results collected 27 years ago (PWR, unpublished data) on *M. sanguinipes* and *M. packardii* Scudder is presented.

MATERIALS AND METHODS

Data were gathered separately by the authors. In studies by WC, the following field populations were sampled. Fourth and fifth instars of *M. sanguinipes* were collected near Bethune, Saskatchewan (Bet); Rigaud, Quebec (Que); and Green Mountain Road, British Columbia (BC) during the spring and summer of 1981. Insects were sexed, separated and allowed to mature in laboratory cages until commencement of matings. Adult *M. sanguinipes* were sampled from West Lafayette, Louisiana (Lo); Trinity Texas (Tx1); Oakhurst, Texas (Tx2); and Prescott, Arizona (Az) during the spring and summer of 1980. Insects were allowed to

Table 1. Mean (\pm SE) hatchability of field strains and of crosses with nondiapause strains of *Melanoplus sanguinipes* (NDwc and NDpr) and *M. packardii* (NDpr-pac).

Strain	Strain values	Crossed with ND ♀♀	Crossed with ND ♂♂
NDwc	78.8 \pm 2.4 (111) ^a	—	—
Bet	0.3 \pm 0.3 (22)	87.2 \pm 3.4 (26)	22.4 \pm 5.9 (31)
Que	2.6 \pm 1.3 (36)	54.0 \pm 5.1 (43)	0.0 \pm 0.0 (11)
BC	25.2 \pm 4.5 (49)	79.4 \pm 6.3 (24)	5.1 \pm 2.8 (7)
Lo	30.4 \pm 6.4 (38)	55.3 \pm 5.9 (42)	42.7 \pm 8.6 (24)
Tx1	38.9 \pm 6.9 (21)	50.7 \pm 8.2 (14)	21.7 \pm 13.6 (5)
Tx2	30.6 \pm 13.6 (7)	70.5 \pm 7.6 (21)	9.7 \pm 7.6 (8)
Az	38.7 \pm 6.8 (34)	91.8 \pm 2.6 (22)	43.1 \pm 7.4 (28)
NDpr	81.7 \pm 2.7 (100)	—	—
Wyn	NA	83.5 \pm 2.7 (61)	23.1 \pm 2.3 (168)
NDpr-pac	76.4 \pm 1.5 (305)	—	—
Dav	26.2 \pm ^b (49)	68.9 \pm 4.9 (53)	25.8 \pm 3.4 (67)

^a n = number of pods.

^b—no standard error because pods hatched in groups.

NA—not available.

deposit eggs in cages available in the laboratories of resident colleagues (see Acknowledgment). Harvested eggs (F_1 of field animals) were sent to the University of Regina and the emergent offspring used for these studies. All strains were crossed reciprocally with the nondiapause strain (NDwc) developed by Pickford & Randell (1969) beginning with material collected near Delisle, Saskatchewan (Pickford 1958). In addition, two of the above field populations, Que and BC, were mated reciprocally. Experimental conditions were essentially the same as those in Chapco (1984). About 10 pairs of virgin adults were introduced into standard Hunter-Jones cages. Dead insects were removed and replaced with virgins, if available. Egg pods were collected daily until most or all egg layers were dead and then individually transferred to shell vials with moistened vermiculite and incubated at 30° C for a maximum of 50 days, a length well beyond the period required for the nondiapause strain. Hatchlings were counted daily and removed. Hatchability for each pod was obtained by dividing hatchling number by the total number of eggs, determined by summing the former figure and the number of unhatched eggs.

In studies by PWR, fifth instars of *M. sanguinipes* and *M. packardii* were sampled from Wynyard (Wyn) and Davidson (Dav), Saskatchewan, respectively and allowed to mature in the laboratory. The former was crossed reciprocally (14 pairs) with Pickford and Randell's nondiapause strain (in its 45th generation of selection at the time of the study) and the latter (10 pairs) with a nondiapause strain (in its seventh generation of selection for nondiapause) initiated by PWR. To avoid confusion with NDwc used by WC, the nondiapause strains of PWR are labelled NDpr and NDpr-pac, respectively. Experimental conditions were the same as those of WC except that egg pods were transferred to petri dishes containing moistened filter paper.

Statistical significance of reciprocal differences and of other linear contrasts (see below) was assessed by a modified t -test that takes into account unequal sample variances (Zar 1984), which is the case here. Nonparametric tests of significance

Table 2. Analysis (*t*-tests) of reciprocal differences (maternal effects) and homogenic vs heterogamic mating differences (egg effects).

Strain	Reciprocal differences	ND strain vs ND ♀♀ × field ♂♂	Field strain vs field ♀♀ × ND ♂♂
Bet	***	*	***
Que	***	***	ns
BC	***	ns	***
Lo	ns	***	**
Tx1	ns	**	ns
Tx2	***	ns	ns
Az	***	***	ns
Wyn	***	ns	—
Dav	***	ns	—

ns—not significant.
*—*P* < 0.05.
**—*P* < 0.01.
***—*P* < 0.001.

(Campbell 1967) essentially yielded the same conclusions as the *t*-tests, attesting to the robustness of the latter.

RESULTS AND DISCUSSION

Mean percent hatchabilities along with standard errors are presented in Table 1 for the field strains and reciprocal crosses with nondiapause strains. Hatchabilities for the WC field material ranged from almost 0 (Bet) to 39% (Tx1), far below the value for the nondiapause strain, 79%. A comparison of values for reciprocal crosses suggests a maternal influence on the trait. In general, hatchabilities of eggs laid by nondiapause females mated with field males are consistently greater (significantly so in 5 cases; Table 2) than values for the reciprocal crosses. For example, the hatchability of eggs produced by the cross, NDwc ♀♀ × Bet ♂♂, exceeds the value for Bet ♀♀ × NDwc ♂♂ by about 65%. The phenomenon is apparently not restricted to the nondiapause strain. Que and BC are two field strains that differ in hatchability and exhibit significant reciprocal differences (*P* < 0.01): values for Que ♀♀ × Bet ♂♂ and Bet ♀♀ × Que ♂♂ are 0.7 ± 0.7 (10) and 39.2 ± 9.9 (9), respectively. Analysis of the PWR data on *M. sanguinipes* and *M. packardii* also reveals significant differences between reciprocal crosses (Table 2) adding further support to the claim for maternal effects. It is difficult to assess what these effects really represent. Had all strains been reared under the same conditions, the claim could be made that maternal effects are genotypically mediated on the female parent's side. This conclusion may be valid for the southern populations since insects were uniformly treated (at the University of Regina) and reared from eggs that had been sent although transgenerational effects are not unknown (Sander et al. 1985). In any case, the experimental design precludes a proper separation of genetic and environmental factors that underly the maternal effects.

Despite the ambivalence regarding inheritance and hatchability at the maternal level, a genetic analysis is possible, but at the level of the egg. The availability, on the whole, of two sets of homogamic and heterogamic crosses permits an examination of the possible role of the egg's genotype on hatchability. If maternal

effects, genic or nongenetic, were entirely responsible for the trait, then it would be expected that values would be the same irrespective of the source of the male. To test this possibility, differences between means for crosses with the same maternal type were examined (Table 2, last two columns). Out of a total of nine contrasts involving nondiapause females, there were five significant differences and out of a total of seven contrasts involving field females, there were three significant differences. The magnitude of these differences varies. To illustrate, in the Quebec study, the hatchability of eggs laid by NDwc females mated to Que males is in the same direction as that for the NDwc strain (i.e., indicating a maternal effect), but the value (54%) is significantly less than the value for NDwc (79%). In a few situations the hatchability of F_1 eggs is greater than the corresponding parental value, a result that suggests heterotic effects. For instance, the hatchability associated with the cross, NDwc ♀♀ × Az ♂♂, is 92%, a value significantly greater than the figure for NDwc. It would appear, therefore, that the genotype of the egg can, in some cases, influence its hatchability.

The findings with respect to maternal effects are germane to those wishing to maintain cultures of nondiapause grasshoppers that serve as model systems for purposes of investigating natural populations. It is not uncommon for laboratory strains to experience a reduction in numbers and a subsequent loss of genetic variation, or experience inadvertent selection as a result of adaptation to laboratory conditions. After a number of generations, a laboratory strain may no longer be representative of its species. The problem can be ameliorated to some extent by mating virgin females from the nondiapause strain with field-caught males thereby increasing the storehouse of genetic variation. By virtue of the maternal influence revealed in this paper, the inconvenience that diapause would otherwise present can be circumvented. Indeed, two such "hybrid strains" had been successfully propagated with the Louisiana and Arizona materials for seven generations, when they were terminated.

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